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THE GENERA OF CORVIDAE AND THEIR RELATIONSHIPS

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This paper summarizes a study of the genera of Old World Corvidae undertaken while arranging the collection of the American Museum of Natural History. For completeness the few exclusively New World genera are included. There has been no comprehensive survey of this family since Sharpe's (1909), and many important modern regional lists such as that of Hellmayr (1934) are uncritical in their treatment of genera. Ridgway's (1904) work on the North American genera, while eminently sound, entailed a degree of genus splitting which often obscures relationships. The only species not available to me were *Cyanocitta* ("Cyanolyca") *nana* and *mirabilis*, *Cyanocorax dickeyi*, and *Zavattariornis stresemanni*; the latter is the only genus not examined. My field experience is limited to the genera *Crates*, *Cyanocitta*, "*Aphelocoma*," *Gymnorhinus*, *Pica*, *Nucifraga*, and *Corvus*.

The plan of this paper is similar to that of a preceding one on the Sturnidae (1943, Amer. Mus. Novitates, no. 1247) in which I gave my reasons for favoring the present

trend towards a broad genus concept. Some might prefer the use of subgenera for certain of the lesser groups. Since subgeneric names are indistinguishable in form from generic ones, use of the former, as Dunn (*in* Bogert, *et al.*, 1943, p. 131) recently pointed out, seems to tempt later authors to elevate them to generic status. Accordingly, formal use of subgenera has here been avoided, but where a section of a genus has commonly been referred to under a generic name the latter is used in the discussion, but in quotation marks to indicate that it is not considered to be a valid genus. In other cases, sections of genera are referred to under the name of the included species that was first described. Type species of generic names are given in parentheses after the name of the author. Generic synonyms given include only those with different type species.

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LIMITS OF THE FAMILY CORVIDAE

Although some vertebrate zoologists have thought that the Passeriformes could all be united in a single family, ornithologists have divided this order into 50 or more families. Even so, many aberrant genera have been included in various families at the risk of making them polyphyletic (cf. Mayr, 1943). A compromise involving reduction of some of the present families to subfamilies and their subsequent combination into larger families will probably be the best eventual solution. A beginning was made by Hartert (1910) when he

reduced the babblers, thrushes, Old World flycatchers, and Old World warblers to the status of subfamilies of the Muscicapidae. Another group of closely allied subfamilies can similarly be gathered in the Corvidae. It is beyond the scope of this paper to decide which groups will be included in such an enlarged family Corvidae. They will be essentially what Sharpe (1877, p. 4) called Group Coliomorphae: Corvidae, Paradisaeidae, Oriolidae, Dicteriidae, Prionopidae. The Prionopidae probably do not belong here, while the Cracticidae and

perhaps others are to be added. Accordingly, the Corvidae as generally understood is here considered to be a subfamily, Corvinae. It is true that this group has been divided by some ornithologists into two subfamilies, the Corvinae and Garrulinae, chiefly on the extremely variable and trivial character of tail/wing proportions. Ridgway (1904, p. 204, footnote) although accepting this division, expressed doubt as to whether these groups are actually of subfamily rank. The jays, magpies, nutcrackers, and crows are closely related and agree in all important morphological characters and even in many minor ones, as well as in characteristic behavior patterns.

Hartert (1910, p. 1) and Ridgway (1904, pp. 252-254) give definitions of the Corvidae (Corvinae) which may be consulted by those interested. In general the group is characterized by large size of the included species; nasal bristles; large, strongly scutellated tarsi, booted behind; large tenth (outer) primary; and by a few prevailing types of coloration. The behavior of the Corvinae is equally diagnostic. The following traits are usually present: long-continued courtship feeding; nest building and feeding of young by both male and female; incubation and brooding by female only; burying or hiding of food; breaking of food with the bill while the food is held in the feet; loud and usually harsh notes; omnivorous and more or less predatory feeding habits; bold and inquisitive nature.

Of the genera here included in the Corvinae, the only ones concerning whose allocation there can be any serious doubt are *Platylophus* and possibly *Ptilostomus* and *Zawattariornis*. Life history rather than anatomical studies may well furnish conclusive evidence as to the affinities of these genera.

Stonor (1942) has shown that the New Zealand genera *Callaeas*, *Heteralocha*, and *Philesturnus*, which have sometimes been considered members of the Corvidae, are best considered a separate family, the Callaeidae. It will perhaps prove possible to consider this a subfamily of the Corvidae in the broad sense, for I doubt if the special

relationship formerly postulated between *Heteralocha* and *Philesturnus* and the Sturnidae exists.

Two anomalous Australian genera, *Struthidea* and *Corcorax*, may be allied to the Callaeidae, as several authors have suggested. At any rate they are probably members of the Corvidae in the broad sense, but almost certainly do not belong to the typical Corvinae as here understood. Even if their resemblance to the Callaeidae does not prove to be significant, they are probably more closely related to other subfamilies of the Corvidae occurring in the Australian region than to the Corvinae.

Struthidea and *Corcorax* are sometimes placed in different families, but their similarity in habits (Gould, 1865, pp. 470-473) and in the more conservative features of external morphology leaves little doubt in my mind that they are related and may be placed in a single subfamily, Corcoracinae. The differences between *Struthidea* and *Corcorax* parallel those between *Callaeas* and *Heteralocha* to some extent but are less striking.

Since *Corcorax*, like the chough (*Pyrhcorax*), is large, black, and has a curved bill it received the common name of white-winged chough. Shufeldt (1923) compared skeletons of the two genera and concluded that they are closely related. I am convinced that he was mistaken. Since reliable osteological characters useful in taxonomy are scarce among closely related birds such as comprise the entire order Passeriformes, Shufeldt concentrated upon plastic, adaptive "habitus" characters such as the shape of the bill and associated parts of the skull. Parallelism in such characters was often erroneously considered by Shufeldt to indicate true relationship. He concluded that *Corcorax* is allied to *Pyrhcorax*; that *Cyanocephalus* is a link between the jays and such icterids as *Sturnella*, and that since *Struthidea* has a heavy bill it is profitable to compare it with the neotropical finch *Saltator*. The extreme improbability that the semi-terrestrial *Corcorax* of the Australian bush should have as its closest ally the strong-flying *Pyrhcorax* of the alpine regions of Eurasia was ignored

by Shufeldt, as were many differences in the morphology and habits of the two genera.

The curious West African genus *Picathartes*, which contains two geographically representative species of so-called bald crows, certainly does not belong in the Corvinae and doubtfully in the Corvidae. Elsewhere (1943) I have given reasons opposing Lowe's (1938) suggestion that *Picathartes* is a starling. The habits of the bald crows suggest to me that they may be a very aberrant offshoot of the thrush-babbler assemblage (Walker, 1939).

Although behavior is useful in delimiting the Corvinae as a group from structurally similar subfamilies such as the birds of paradise, great caution must be used in interpreting differences in behavior among members of the Corvinae. A few examples will make this apparent. The Florida race of *Cyanocitta* ("*Aphelocoma*") *coerulescens* is as bold and confiding as a Canada Jay (*Crates*), while the Great Basin race *woodhousei* is furtive and shy. The three species of "*Aphelocoma*" as usually understood, *coerulescens*, *sordida*, and, *unicolor*, are morphologically very similar, except for

variation in wing/tail proportions. Yet *coerulescens* lays spotted eggs, most of its notes are harsh, and it is only moderately gregarious, while *C. sordida* is very gregarious, has a peculiar finch-like call, and lays blue, unspotted eggs. Less is known of the third species, *unicolor*, but it inhabits humid cloud forests (Dickey and Van Rossem, 1938, p. 409), while the other two live in subarid regions. There is also considerable variation in the behavior of some species of the genus *Corvus*. The jackdaw, *C. monedula*, unlike the others, nests usually in hollows of trees or of buildings and lays an egg rather unlike that usual in this genus. *C. typicus* of Celebes was found by Heinrich to be so unlike most crows in voice and habits that Stresemann (1940, p. 16) suggested leaving it in a monotypic genus, but it is so closely related to various other species of *Corvus* of the East Indian region that this procedure is hardly acceptable. *Podoces humilis* nests in rodent burrows and lays white eggs while its congeners build nests in bushes and lay spotted eggs, though some of them occasionally nest in burrows.

VARIABLE CHARACTERS

The Corvinae, though by no means so plastic as their relatives, the birds of paradise, are a variable group. The relative lengths of wing and tail are especially variable, often even in closely related species, as will be apparent from examination of table 1. Since wing and tail lengths often vary independently, the ratio of tail/body and wing/body is given in addition to the usual tail/wing ratios to permit variation in wing and tail to be studied separately. Body length as used here was obtained by subtracting the tail length from the total length, the latter taken from skins, and serves to give a very rough index to general size. The measurements of North American species are from Ridgway (1904), of *Cyanocorax dickeyi* from Moore (1935), of *Zavattariornis* from Moltoni (1938), and of the others from specimens in the American Museum.

One or two examples of variability illustrated in the table may be mentioned. *Kitta chinensis* and *thalassina*, while specifically distinct, are so similar that Chasen (1935, p. 310) called them subspecies of each other. Yet the relative tail length differs greatly. *Cyanocitta coerulescens* has a relatively much shorter wing than the otherwise morphologically similar *sordida* and *unicolor*.

The crest is also extremely variable in the Corvinae. For example, in the *beechei* superspecies of *Cyanocitta* ("*Cissolopha*"), *san-blasiana* has a prominent frontal crest absent in the other three species of the group. The remarkable range of structure in the crest exhibited by various species of the genus *Cyanocorax* is described in the discussion of that genus below.

Of the 19 genera here recognized no

SPECIES	TAIL/WING	TAIL/BODY	WING/BODY	BODY
<i>Platylophus galericulatus</i>	86	69	81	180 mm.
<i>Garrulus glandarius</i>	83	92	110	175
" <i>lanceolatus</i>	111	106	96	155
" <i>lidghi</i>	111	114	113	180
<i>Cyanocitta cristata</i>	98	94	96	137
" <i>coerulescens insularis</i>	110	99	90	150
" <i>sordida</i>	87	95	111	153
" <i>unicolor</i>	95	99	104	156
<i>Gymnorhinus cyanocephalus</i>	74	72	97	159
<i>Cyanocorax violaceus</i>	83	78	94	212
" <i>cristatella</i>	73	79	108	190
" <i>heilprini</i>	100	90	90	195
" <i>chrysops</i>	111	96	86	175
" <i>mystacalis</i>	109	107	98	145
" <i>dickeyi</i>	95	—	—	—
" <i>luxuosa</i>	130	125	96	138
<i>Calocitta formosa</i>	161	171	79	179
<i>Kitta thalassina</i>	87	85	98	143
" <i>chinensis</i>	145	136	94	165
" <i>whiteheadi</i>	113	124	110	200
" <i>erythrorhyncha</i>	200	205	103	190
<i>Platysmurus leucopterus</i>	110	122	112	173
<i>Ptilostomus afer</i>	172	166	97	165
<i>Podoces biddulphi</i>	72	61	86	177
<i>Nucifraga columbiana</i>	60	63	105	186
<i>Zavattariornis stresemanni</i>	93	100	107	135
<i>Pyrhocorax pyrrhocorax</i>	56	70	126	220
<i>Corvus corax</i>	56	61	109	402

TABLE 1. Proportions and body lengths of some species of the Corvinae. The body length is given to supply a rough index to general size.

fewer than eight are monotypic. Three of the eight monotypic genera are so distinct and aberrant that there is some question whether they belong to the Corvinae

(*Platylophus*, *Zavattariornis*, *Ptilostomus*). Despite the large percentage of monotypic genera, the average of about five species per genus is fairly satisfactory.

Corvidae

CROWS, BIRDS OF PARADISE, OLD WORLD ORIOLES, ETC.

Corvinae

CROWS, MAGPIES, JAYS, NUTCRACKERS, ETC.

PLATYLOPHUS SWAINSON (GALERICULATUS)

SHRIKE JAY

SPECIES: 1, *galericulatus*.

RANGE: Malay Peninsula, Sumatra, Java, Borneo.

DIAGNOSIS: Plumage brown or black with white crescents on the sides of the neck; a few of the occipital feathers greatly elongated and broadened near their tips, thus forming a large crest; nasal bristles sparse and short; rictal bristles exceptionally long; tip of mandible more hooked than in other jays; bill otherwise like that of *Garrulus*.

REMARKS: *Platylophus* has usually been considered a member of the Laniidae, but this is evidently incorrect. Bartels and Stresemann (1929, p. 136) place it in the Corvidae and state that its habits and nidification are jay-like but give no details. More evidence is needed.

Of the three Old World genera of jays, one is boreal, one temperate, and the present one tropical, in distribution. I do not consider this an argument against allocation of *Platylophus* to the jays, as the New World jays are concentrated in the tropics. Probably other jays once existed in the

tropics of Asia but have been displaced by the more specialized magpies. *Platylophus*, though in some respects aberrant, may be primitive. Partly to express this and partly because knowledge of *Platylophus* is still insufficient, it is placed at the beginning of the Corvinae.

**CRACTES BILLBERG (PERISOREUS AUCT.)
(INFAUSTUS)**

CANADA JAY, ETC.

SYNONYMS: *Boanerges* Thayer and Bangs (*internigrans*).

SPECIES: 1, *internigrans*; 2, *infaustus* (including *canadensis* and *obscurus*, considered by some to be specifically distinct).

RANGE: Boreal regions of Northern Hemisphere, south in the mountains to western China and California.

DIAGNOSIS: Color varying from black to grayish white, sometimes rufous; plumage soft and fluffy; bill rather short and somewhat depressed.

REMARKS: The interesting *internigrans* of the mountains of western China suggests *Garrulus lanceolatus* of the Himalayas in its bill and black head. Though it is larger and has relatively stronger bill and legs than *infaustus*, it is unnecessary to recognize *Boanerges*, as Stegmann and others have already concluded. The unspecialized appearance of *Cractes* may be in part secondary adaptation to its boreal habitat, but the genus is rather primitive. The resemblance of *internigrans* to *Garrulus* and the occurrence of both species of *Cractes* in Asia leave little doubt that it is an Old World genus which reached America recently, later than the other American jays.

GARRULUS BRISSON (GLANDARIUS)

EUROPEAN JAY, ETC.

SYNONYMS: *Laletris* Reichenow (*lanceolatus*); *Lalocitta* Reichenow (*lidthi*).

SPECIES: 1, *glandarius*; 2, *lanceolatus*; 3, *lidthi*.

RANGE: Palaearctic region and Amami-Oshima and Tokuno-shima Islands, Ryu Kyu Group, south of Japan (*lidthi*).

DIAGNOSIS: Alula and sometimes remiges and rectrices blue barred with black; body plumage reddish or vinaceous; wings and tail bluish black; size large for jays.

REMARKS: As compared with *glandarius*, *lidthi* is specialized in the following respects: size larger; bill coarser, less upturned; coloration brighter; remiges and rectrices tipped with white; throat feathers lanceolate; tail relatively longer (table 1). The third species, *lanceolatus* of the Himalayas, is intermediate in almost every respect. The specialization of *lidthi* is, it would seem, to be attributed to its isolation on two small tropical islands. The three species obviously comprise a natural group comparable with other genera of jays; this is concealed and nothing gained by placing each of the three in a monotypic genus. That *lidthi* is more specialized and magpie-like than *glandarius* seems to me self-evident. Sushkin (1927), however, reached the surprising conclusion that *lidthi* is a primitive species representing stock ancestral to both the New and Old World jays and surviving on segments of a former intercontinental land bridge which he called Behringia. This suggestion seems to have been based upon theories concerning land bridges rather than upon the actual characters of *lidthi*.

Jahn (1942, pp. 79-82) found *lidthi* to be essentially like *glandarius* in habits, except that it nests in holes in trees. A substantial nest is built, and one or two nests have been found in the open in thick cover—indications that the hole nesting of *lidthi* is of recent origin. The number of eggs laid is less than in *glandarius*; this may represent the reduction usual in tropical species rather than an adjustment to lack of enemies as Jahn suggests. The eggs of *lidthi*, unlike those of *glandarius*, are unspotted and blue. This variation in egg color is similar to that existing between *Cyanocitta sordida* and other species of *Cyanocitta*.

The colored map of the distribution of the various forms of *Garrulus* which forms the frontispiece of Wallace's "Island life" (1881) is still of interest. Since then some of the forms have been subdivided into minor subspecies; it has been learned that the true home of *lidthi* is the Ryu Kyu Islands, not southern Japan, and that the only member of the genus which overlaps

the range of others without hybridizing is the distinct species *lanceolatus*. Wallace (*op. cit.*, p. 23) thought that because *Garrulus* occurs from the British Isles to Japan and Formosa and yet is absent from many apparently suitable districts and is nowhere abundant, it is a "decaying" genus. This accords with the belief that the jays are in general a primitive group in process of displacement by more specialized corvids, but I am by no means sure that the facts mentioned by Wallace are reliable indications that *Garrulus* is a decadent genus.

THE AMERICAN JAYS

The approximately 32 species of American jays are, with the possible exception of *Gymnorhinus*, a closely related monophyletic group. The facts would be better expressed by placing them all in one genus than by splitting them into nine as was done by Ridgway (1904). An intermediate course is here followed, and four genera are recognized. These I believe are natural and monophyletic, but their characters are very trivial, intergrading, and variable, and later opinion may dictate further reduction. The assemblage may, by relying on a combination of characters, be split into two large genera, *Cyanocitta* and *Cyanocorax*, the latter slightly more specialized. Two additional genera, *Psilorhinus* and *Calocitta*, containing but a species or two each, must then also be upheld to retain a semblance of consistency in evaluating the characters of the group.

CYANOCITTA STRICKLAND (CRISTATA)

BLUE JAY, ETC.

SYNONYMS: *Aphelocoma* Cabanis (*californica*, a race of *coerulescens*); *Cissolopha* Bonaparte (*san-blasiana*); *Cyanolyca* Cabanis (*armillatus*, a race of *viridi-cyana*); *Garrulina* Gray (*unicolor*); *Lophocorax* Kaup (*diademata*, a race of *stelleri*); *Sieberocitta* Coues (*arizonae*, a race of *sordida*).

SPECIES: 1, *cristata*; 2, *stelleri*; 3, *coerulescens*; 4, *sordida*; 5, *unicolor*; 6, *pumilio*; 7, *nana* (not seen); 8, *mirabilis* (not seen); 9, *argentina*; 10, *viridi-cyana*; 11, *turcosa*; 12, *pulchra*; 13, *melanocyanea*; 14, *yucatanica*; 15, *san-blasiana*; 16, *beecheii*.

RANGE: Alaska and southeastern Can-

ada to western South America as far as Peru and Bolivia.

DIAGNOSIS: As compared with *Garrulus*, *Cyanocitta* differs as follows: no reddish or vinaceous in plumage; instead prevalently blue or blue and black; usually without black bars on remiges and rectrices, when present they do not occur on the alula as in *Garrulus*; mandible less upturned, or not at all so; size usually smaller, body slenderer. *Cyanocitta* is much more closely related to the other American jays than to *Garrulus*, but is in general less specialized (see below).

The genus *Cyanocitta*, as thus delimited, contains the following sections:

1. *Cyanocitta* in the restricted sense contains two species, *cristata* of eastern, and *stelleri* of western North America. Unlike other members of the genus, they have occipital crests and black bars on the wings and tail. It is perhaps justifiable to consider the two as forming a super-species, but *cristata* is somewhat more specialized than *stelleri* in color pattern.

2. "*Aphelocoma*," which contains the single species *coerulescens* (unless *californica* and *insularis* are considered specifically distinct), lacks the crest and black wing and tail bars of the preceding group. The wing is relatively shorter. It occurs in Florida, the southwestern United States, and Mexico.

3. "*Sieberocitta*" (including "*Garrulina*") includes two species, *sordida* and *unicolor*, which are usually referred to "*Aphelocoma*." They have a relatively longer wing than *coerulescens* or even *cristata*. *C. sordida* is more gregarious than *coerulescens*, has a finch-like note, and lays unspotted blue eggs. Less is known of *unicolor*, but unlike either of the other species mentioned it occurs in cloud forests, not semiarid regions. In proportions it is similar to *sordida*. This group ranges from Arizona to Central America.

4. The "*Cyanolyca*" group contains species 6-12, which occur from southern Mexico to western South America as far as Peru and Bolivia. They are much like the preceding two sections but have the black

eye stripe expanded into a mask. Often there is a light area on the nape and a crescentic mark across the breast like that of *C. cristata*. The frontal feathers are usually bristly or velvety.

5. "*Cissolopha*" contains the four species 13-16, which are closely related and evidently comprise a single superspecies. They have a heavier and more magpie-like bill, and the entire head and at least the anterior half of the underside are black. The group occurs from northern Mexico to Central America.

It is significant that four of the five groups are represented in Central America by forms that are primitive and similar to one another. These are *stelleri* (southern races), *unicolor*, *pumilio* (and *nana*), and *melanocyanea*. Furthermore, "*Cissolopha*" *pulchra*, which also occurs in Central America, is a link between "*Cyanolyca*" and "*Cissolopha*." It has the pattern of the former, but the heavy bill and to some extent the blackish head region of the latter. *C. pumilio* and *nana* similarly connect the "*Aphelocoma*"-"*Sieberocitta*" groups with "*Cyanolyca*." As Ridgway (1904, p. 324) pointed out they are structurally the same, while the color difference is much less than would be inferred from Ridgway's remarks. In fact Salvin and Godman (1879-1904, pp. 407-414) placed *nana* in "*Aphelocoma*" and considered "*Cissolopha*" a synonym of "*Cyanolyca*." *C. cristata* and *stelleri* are essentially similar to "*Aphelocoma*" in habits, and they should not be separated generically on such an extremely trivial basis as the presence or absence of a crest. The similar variation in the crest in "*Cissolopha*" among forms which Hellmayr (1934, p. 37) has even suggested may be subspecies (though I do not agree) was noticed above.

To summarize, although it is possible to subdivide the enlarged genus *Cyanocitta* into five sections, most of these contain but a single species or superspecies, and all of them are characterized by extremely variable and intergrading characters. All twelve of the species are similar in most respects, so it seems preferable to unite them in one genus.

GYMNORHINUS WIED (CYANOCEPHALUS)

PIÑON JAY

Brodkorb (1936, p. 1) is evidently correct in stating that *Gymnorhinus* Wied is not a homonym of *Gymnorhina* Gray and hence must be used for the piñon jay rather than *Cyanocephalus* Bonaparte.

SPECIES: 1, *cyanocephalus*.

RANGE: Southwestern United States and northern Lower California.

DIAGNOSIS: As compared with *Cyanocitta*: color nearly the same as in *C. sordida*; tail shorter; wing more pointed; flight stronger; bill longer and almost straight, slightly depressed towards its tip; nasal bristles lacking.

REMARKS: Though much like *C. sordida*, *Gymnorhinus* resembles *Nucifraga* also, as regards bill shape and proportions (although the tail is not quite so short). It has generally been placed with the crows and nutcrackers, not with the jays. I am inclined to consider the piñon jay a specialized American jay which parallels *Nucifraga columbiana* somewhat because of similarity in feeding habits. Both species feed on piñon cones, and I have seen them feeding together in the same woods in large numbers. A jay thus specialized for feeding on the cones of a tree which fruits irregularly and is discontinuous in distribution would require strong flight. The difference in relative wing length between *Cyanocitta coerulescens* and *sordida* is as great as that in tail length between the latter and *Gymnorhinus*. The absence of rictal bristles in the piñon jay is not surprising if it is an American jay, in which they are absent in some other genera, but is remarkable if it is a relative of the boreal nutcrackers. Nor is the blue color of *Gymnorhinus* suggestive of either species of *Nucifraga*, though it might, it is true, be a reversion to the coloration of the Old World jays ancestral to *Nucifraga*. The fact that the latter has its most specialized representative in the Old World suggests that it, like all the other more specialized corvine genera, is of Old World origin. There is a slight possibility, however, that *Nucifraga* is of New World origin and

that *Gymnorhinus* is a true link between it and the more primitive *Cyanocitta*.

As regards habits, *Cyanocephalus* does not share the very early nesting season of *Nucifraga*, though the eggs of the two are rather similar. However, egg color varies greatly in *Cyanocitta*. Some jays of the genus *Cyanocorax* lay eggs similar to those of *Nucifraga*. The shrill flock note of the piñon jay suggests that of the Arizona jay, but certain notes of the former have been likened to those of crows or nutcrackers.

Comparison of a skull of *Gymnorhinus* with those of *Nucifraga*, *Garrulus*, *Cyanocitta*, and *Corvus* reveals that *Gymnorhinus* shares with *Nucifraga* a narrowing of the anterior part of the skull, correlated with the chisel-shaped bill. This is probably entirely adaptive. *Gymnorhinus* agrees with *Cyanocitta* and *Garrulus* in having the post-frontal and the squamosal process less prominent than in *Nucifraga* or *Corvus*, but this may be correlated with their smaller size. The skulls of all these species are very similar. Shufeldt's (1888) study of the skeletons of American Corvidae unfortunately did not include *Nucifraga*. Though he states in his conclusions that osteologically *Gymnorhinus* is a link between *Cyanocitta* and *Corvus*, in the actual comparisons of skeletal elements, wherever a difference exists between the two, he found *Gymnorhinus* to agree with *Cyanocitta* (pp. 330, 333, 341, 343).

While I believe that a preponderance of evidence indicates relationship of *Gymnorhinus* to *Cyanocitta* rather than to *Nucifraga*, it must be remembered that *Nucifraga* itself is only a specialized offshoot of the (Old World) jays.

PSILORHINUS RÜPPELL (MEXICANUS)

BROWN JAYS

SPECIES: 1, *mexicanus*; 2, *morio*. The two species occur together and are very similar. They may prove to be representatives of a single species, but this is unlikely (cf. Wetmore, 1943, p. 297).

DIAGNOSIS: Similar to the larger, coarser species of *Cyanocitta* ("*Cissolopha*" group) but structurally coarser; nasal bristles sparse; plumage dull brownish or dirty white. *Psilorhinus* has a crop-like

furcular sac formed by a diverticulum of the clavicular air sac and used in producing a snapping sound (Sutton and Gilbert, 1942, p. 165).

REMARKS: *Psilorhinus* seems to be secondarily coarsened in structure and simplified in coloration until it is difficult to tell if it is more nearly related to the larger species of *Cyanocitta* such as *beechei* or to *Cyanocorax* (as Salvin and Godman thought). Accordingly it is here placed between them, as the only logical alternative would be to unite the three genera. The furcular sac may be the best generic character of *Psilorhinus* as Sutton and Gilbert (*tom. cit.*) intimate.

CYANOCORAX BOIE (CHRYSOPS)

GREEN JAY, ETC.

SYNONYMS: *Coronideus* Cabanis (*violaceus*); *Uroleuca* Bonaparte (*cristatella*); *Xanthoura* Bonaparte (*yncas*).

SPECIES: 1, *caeruleus*; 2, *cyanomelas*; 3, *violaceus*; 4, *cristatella*; 5, *heilprini*; 6, *cayanus*; 7, *affinis*; 8, *cyanopogon*; 9, *chrysops*; 10, *mystacalis*; 11, *dickeyi*; 12, *yncas*.

RANGE: Southern Texas to Argentina.

DIAGNOSIS: Like *Cyanocitta* but in general more specialized; crest usually present but extremely variable; throat, breast, and usually large areas on sides and top of head black; the black breast more sharply demarked from the remainder of the underside than in any species of *Cyanocitta*; lower breast and abdomen and large areas in the tail characteristically white or yellow but sometimes blue or purple; size averaging larger and body form, legs, and feet more robust than in *Cyanocitta*.

REMARKS: *Cyanocorax* can be subdivided into the following sections:

A. The "*Coronideus*" group contains species 1-3, which occur in eastern South America. They are characterized by robust form and by a simple color pattern in which the abdomen and tail lack white and the head is entirely black. This group, although most like the more primitive *Cyanocitta* in coloration, is atypical by reason of its robust form, and in view of its distribution may be a side branch of the genus. "*Coronideus*" has not usually been recognized.

B. "*Uroleuca*" is usually treated as a monotypic genus characterized by the recurved crest of the single species *crisatella*. This species combines the robust form and black head of the "*Coronideus*" group with the white abdomen and white-tipped rectrices of the restricted *Cyanocorax* section. It occurs on the Brazilian tableland, suggesting relationship with the "*Coronideus*" group.

C. The restricted *Cyanocorax* section contains species 6-11, which occur in southern Sinaloa and from Central America to western South America as far as Peru. In this group the body is slenderer and the tail relatively longer; the abdomen and end of the tail are white or yellowish, and there is a characteristic head pattern of blue or white marks above and below the eyes, the lower one extending over the malar region. The rare *C. heilprini* of the Brazil-Venezuela borderland is so nearly intermediate between this and the "*Coronideus*" group that it cannot be included in either. It has the purple under parts of the "*Coronideus*" section, but the abdomen is whitish posteriorly, and there are narrow white tips on the rectrices; the head pattern is only partly developed, and the form is slender.

D. "*Xanthoura*" is another monotypic group; the sole species, *yncas*, ranges from southern Texas to Peru. It is even more slender in appearance, perhaps because its tail is relatively longer (see table 1 for proportions of this and other species of the genus). The under parts and lateral rectrices of *yncas* are bright yellow; the upper parts and central rectrices are green, washed with blue in some races; the frontal crest, as well as the usual marks on the face, is blue; the size is small.

The commonest type of crest in *Cyanocorax* is composed of bristly, narrow feathers, which are short in *cyanomelas* but longer in *heilprini* and others. In some species such as *yncas* the crest is essentially similar but the feathers somewhat softer. In *crisatella* the feathers of the crest are much longer and curved back over the crown. *C. cyanopogon* has a frontal crest of the usual type, and in addition the occipital feathers are lengthened and broad-

ened to form a short, full crest which overhangs the white nape. As an example of the frequent parallelism which suggests that all genera of the Corvinae are rather closely allied, it may be mentioned that the Malaysian magpie, *Platysmurus*, has two similar crests. The type species *chrysops* is unique in that the feathers of the entire top of the head are bristly or velvety and not merely the frontal feathers. In *dickeyi* the crest is said to include the crown but not the occiput as in *chrysops*. Moore (1935, p. 275, pl.) described the crest of *dickeyi* as a "straight, stiff and erect crest, which tends to segregate at the apex into numerous tufts of stiff, narrow and unusually elongated feathers. . . ." In *chrysops* the form of the crest varies considerably among the subspecies.

Cyanocorax dickeyi, which I know only from the published plate and photographs, is a member of the restricted *Cyanocorax* group. It resembles *mystacalis* of Ecuador by having the head pattern white, the back blue (though not of exactly the same shade), and the tail extensively white. In *dickeyi*, however, even the lateral rectrices have dark bases, while in *mystacalis* they are entirely white. Presumably one must admit *dickeyi* to be closer to *mystacalis* than to any other species of the genus despite the more than 3000 miles which separate their ranges. Captain Delacour tells me he would consider them representatives of a single species or super-species, but, aside from the geographical improbability of this, the striking differences in general size and in the crest are almost certainly of specific importance. I think it is possible that, in this assemblage of closely related species in which a few common characters occur in different combinations, this may be another instance of parallelism. At any rate, it seems misleading when Moore (1935, p. 277) states that *dickeyi* is furthest in characters from the geographically nearest species, *affinis*, which ranges north to Costa Rica. *C. dickeyi* may be as nearly related to *affinis* as to any other living species except (probably) *mystacalis*, and is, in my opinion, closer to *affinis* than to *heilprini* or *violetaceous*, species which Moore mentions as

resembling *dickeyi* in some respects. He might also have pointed out when emphasizing the territorial gap between *dickeyi* in Sinaloa and its congeners in Central and South America that the intervening area is occupied by "*Xanthoura*," which is obviously a *Cyanocorax* in essential characters, and by *Calocitta* and *Psilorhinus*, both of which are apparently offshoots of *Cyanocorax*. The American jays are concentrated in Middle America. Presumably competition is thereby increased, and it is possible that the small, isolated range of *dickeyi* is somehow correlated with this fact.

From the above discussion it will be apparent that *Cyanocorax*, as here understood, can be subdivided only by resorting to extremely variable characters. "*Coronideus*" with its simple coloration and robust form is perfectly united with the more typical members of the genus by *crisatella* and *heilprini*. The crest is so extremely variable in this group that it is inconsistent to maintain "*Uroleuca*" on this basis. Nor does the green back, yellow abdomen (the latter shared by the type species, *chrysops*), and long tail of *yncas* conceal the fact that it is a close ally of *chrysops*. The problem for one who would like generic characters to be more stable and substantial than specific characters is not whether to unite the above species in *Cyanocorax*, but how to keep *Cyanocorax* separate from *Psilorhinus*, *Calocitta* and, for that matter, *Cyanocitta*.

CALOCITTA GRAY (FORMOSA)

MAGPIE-JAYS

SPECIES: 1, *formosa*. The form *colliei* is considered specifically distinct by some authors.

RANGE: Mexico and Central America.

DIAGNOSIS: Essentially like *Cyanocorax*, but tail very long and graduated; some of the crown feathers much elongated and somewhat spatulate, forming a conspicuous crest; size large.

REMARKS: In view of the great variability in proportions and crests existing in the genus *Cyanocorax*, it is doubtful whether *Calocitta* should be kept separate. In *Calocitta f. colliei* we find the following unmistakable signs of close affinity with

Cyanocorax: black throat and breast; white abdomen; similar head pattern and white in the lateral rectrices. In *C. f. formosa* the black throat and breast are absent except for a black bib similar to, and homologous with, that of *Cyanocitta cristata* and some other species of *Cyanocitta*. As noted above in discussing *Cyanocorax*, *Calocitta* has perhaps replaced more primitive earlier Mexican species of the former.

THE TRUE MAGPIES

Although the New World jays have given rise to some magpie-like types, notably *Calocitta*, the intergradation with the jays is so complete that no line can be drawn. In the Old World magpies there is a more definite gap separating them from the jays. *Garrulus lidthi*, however, has acquired some magpie-like characters and is quite similar to *Kitta*, especially *Kitta ornata*.

KITTA TEMMINCK (CHINENSIS)

GREEN MAGPIES, ETC.

SYNONYMS: *Cissopica* Delacour (*whiteheadi*); *Urocissa* Cabanis (*erythrorhyncha*).

SPECIES: 1, *thalassina* (and geographical representatives); 2, *chinensis*; 3, *whiteheadi*; 4, *ornata*; 5, *flavirostris*; 6, *erythrorhyncha*; 7, *caerulea*.

RANGE: India and Ceylon to China and Formosa south through the Malay Peninsula and Greater Sunda Islands.

DIAGNOSIS: As compared with *Garrulus*: structure coarser; size usually larger; tail more graduated and usually longer; bill, legs, and feet heavier and red or yellow in color (legs blackish in *whiteheadi*); nostrils exposed; nasal bristles sparse or absent. Differs from other magpies by the coarser, heavier bill, by having the bill red, and in other respects noted later.

REMARKS: This genus divides naturally into four sections:

A. *Kitta* proper contains two species, *thalassina* and *chinensis*, distinguished by small size; greenish or yellowish coloration which fades rapidly after death; coronal feathers lengthened, forming a crest; a black eye stripe which extends back beneath the crest; eyelids wattled and

brightly colored. These species occur in dense mountain jungle in southeastern Asia and adjacent islands. As Delacour (1929, p. 3) indicated in his key to this group there are two natural divisions: (1) those in which the tertials are white-tipped and have a subterminal black spot, and the tail is relatively longer (*chinensis*), and (2) those lacking these characters (superspecies *thalassina*). Whether the forms of group (2), all of which are geographically representative, are considered subspecies, or, in the more differentiated forms, species, is a matter of opinion. The members of group (2) from south (Java) to north (Hainan) are: *thalassina*, *jefferyi*, *hypoleuca*, *chauleti*, *concolor*, *jini*, and *katsumatae*. Peters (1940, p. 203) has already pointed out that Chasen (1935, p. 310) was in error in considering *jefferyi* and *thalassina* races of *chinensis*.

B. *K. ornata* of Ceylon has the eyelids wattled like the preceding group to which it has usually been referred, but it is closer to the following group, "*Urocissa*," with which it has in common concolorous head and breast, longer tail and coloration which lacks the evanescent qualities of that of the *Kitta* group. *K. ornata* differs from both *Kitta* and "*Urocissa*" by having the head, breast, and remiges bright rufous.

C. "*Urocissa*" includes *flavirostris*, *erythrorhyncha*, and *caerulea*. This section differs from *ornata* by lacking the wattled eyelids; the tail is even longer and the head, breast, and remiges are black or blue. The first two species are similar; *caerulea* of Formosa is probably a representative of one of them, but it is difficult to say which. *K. caerulea* is much bluer than either of the mainland forms and has a heavier bill.

D. "*Cissopica*," which contains only *whiteheadi*, was characterized by Delacour (1927, p. 164) as follows: "Differs from *Urocissa* in having a much coarser and more powerful bill and legs and a shorter tail. . . . General plumage grey, black and pale yellow, never blue. I chose the name of this new genus to show the affinity of these birds to the *Cissa* [group A above] which

they exactly resemble in their voices and actions." Captain Delacour informs me that he now considers it preferable to include *whiteheadi* in *Kitta*, though it forms a distinct subgroup. *K. whiteheadi* is coarsened and simplified in coloration just as is *Psilorhinus* in the New World. The black breast and lighter abdomen of the "*Urocissa*" group are suggested in *whiteheadi*, and it also agrees with this group in its large size and coarse structure. However, it resembles the restricted *Kitta* group in some details as well as in habits and may be a link between it and "*Urocissa*."

The enlarged genus *Kitta* contains a natural assemblage of only seven species. The immediate common ancestry of all these species is obscured if they are placed in three or four genera.

CYANOPICA BONAPARTE (CYANUS)

AZURE-WINGED MAGPIE

SPECIES: 1, *cyanus*.

RANGE: Iberian Peninsula and eastern temperate Asia north to Japan and Siberia. (For a map of this remarkable instance of discontinuous distribution see *Ibis*, 1928, vol. 25, opp. p. 532.)

DIAGNOSIS: Coloration blue and white and rectrices white-tipped as in some species of *Kitta*; bill black and shaped as in *Pica*; nasal bristles well developed as in *Pica*; form slenderer, size smaller, legs weaker, plumage silkier than in either *Kitta* or *Pica*; nest open as in *Kitta*; primarily arboreal. *Cyanopica* connects *Kitta* and *Pica* in some respects, but is too distinctive to be united with either.

PICA BRISSON (PICA)

COMMON MAGPIE

SPECIES: 1, *pica*.

The yellow-billed magpie, *nuttalli*, of California is considered by many distinct enough to warrant specific status in the same superspecies as *pica*. Some of the Old World races at times build their nests at considerable heights in tall trees as does *nuttalli*. Yellow-billed individuals have occurred as sports in some of the Old World races. Coues' (1894, p. 421) statement that *nuttalli* is a "perpetuated accident" of *P.*

p. hudsonica is in keeping with present opinion as to the frequent fixation of non-adaptive characters in isolated populations.

RANGE: Palaearctic region and western North America.

DIAGNOSIS: Outer primary falcate; a distinctive color pattern of white and metallic bluish or greenish black; throat feathers lanceolate; nest domed, often with two entrances, with an interior cup of mud; feeds much on the ground, where it progresses mostly by walking. *Pica* is nearest to *Cyanopica* with which it shares characters mentioned in diagnosing that genus and also some details of coloration. It is less closely related to *Crypsirina* (including "*Dendrocitta*"). *Pica* is obviously an Old World genus that has reached North America relatively recently. Probably it will eventually adjust itself to conditions in eastern North America, since in the Old World it occurs both in semiarid and in humid regions.

CRYPsirina Vieillot (TEMIA)

RACQUET-TAILED AND TREE MAGPIES

SYNONYMS: *Dendrocitta* Gould (*leucogaster*); *Temnura* Temminck (*temnura*); *Vagabunda* Kaup (*vagabunda*).

SPECIES: 1, *vagabunda*; 2, *frontalis*; 3, *leucogaster*; 4, *occipitalis*; 5, *formosae*; 6, *bayleyi*; 7, *temia*; 8, *cucullata*; 9, *temnura*.

RANGE: India, southern China, and Formosa south through the Greater Sunda Islands to Bali.

DIAGNOSIS: Bill black, short, heavy, strongly arched, nasal bristles short but dense; color variegated brown, white, gray, or black but not blue, sometimes wholly black; frontal feathers short and velvety, especially in *temia* and *cucullata*; legs black and relatively smaller than in *Kitta* or *Pica*; proportions about as in *Pica*; nest open; primarily arboreal, hopping when on the ground.

REMARKS: This genus has the following three easily separated sections:

A. "*Dendrocitta*" contains species 1-6. Its characters are as for the genus; the rectrices are normal.

B. *Crypsirina* proper contains *temia* and *cucullata* characterized by smaller size; spatulate central rectrices; velvety

frontal plumes and silky plumage. *C. cucullata* has a pattern much like members of the preceding group, but *temia* is entirely black.

C. "*Temnura*" contains only *temnura*, which has a restricted range in part of Indo-China. This species has rectrices that are incised along their edges and truncated at their tips as though bites had been taken from them. *C. temnura* is entirely black like *temia*, but the plumage is not so soft.

In various species of "*Dendrocitta*" the rectrices increase in width distally, thus foreshadowing the spatulate condition. This is especially true of *bayleyi* of the Andaman Islands, a species whose small size also suggests *temia* and *cucullata*. The increase in width of the central tail feathers distally in *bayleyi* is as follows in four specimens:

Width of feather near center: 19, 20, 20, 22 mm.
Width of feather near tip (specimens in same order): 23, 29, 29, 26 mm.

In *temia* the spatulate rectrices measure about 17 mm. across at the center and 39 mm. at the tip. The difference in feather shape involved is only a matter of degree and, other things being equal, would be of no more than subspecific value. *C. temia* is also specialized slightly by reason of its small size, silky black plumage, and especially the velvety frontal feathers which cover the nostrils and take the place of nasal bristles. However, *cucullata*, which agrees with *temia* in size, presence of spatulate rectrices, and has always been placed in the same genus, is intermediate as regards coloration and nasal bristles between the restricted *Crypsirina* and "*Dendrocitta*" groups. In view of the close relationship and minor distinctions of these two groups, it seems that the facts will be best expressed by considering *Dendrocitta* a synonym of *Crypsirina*. It is unfortunate that the latter name has priority over the better-known *Dendrocitta*. But for this, the two would probably have been united before now.

The little-known species *temnura* is a member of the *Crypsirina* group in the broad sense. The tail is variable in this genus, so it seems justifiable to include

"*Temnura*" in *Crypsirina*. Moreover, *temnura* links *Crypsirina* and "*Dendrocitta*" in some respects, just as *bayleyi* does in others. *C. temnura* has the black coloration of *temia*, but the coarser plumage and nasal bristles of "*Dendrocitta*." Its size is intermediate as shown by the following sample wing lengths of the species most important in defining the limits of *Crypsirina*: *temia*, 118; *bayleyi*, 121; *temnura*, 137; *leucogaster*, 148 mm.

**PLATYSMURUS REICHENBACH
(LEUCOPTERUS)**

WHITE-WINGED MAGPIE

SPECIES: 1, *leucopterus*.

RANGE: Malay Peninsula, Sumatra, Borneo.

DIAGNOSIS: Differs from *Crypsirina* thus: frontal feathers bristly and elongated, forming an erect crest; feathers of occiput elongated and broadened, forming a short, full crest distinct from the frontal one; rictal bristles long; rectrices not spatulate; tail relatively shorter and less graduated; form more robust; plumage black with the exception of a white streak on the wing.

Platysmurus is a close ally of *Crypsirina* as shown by the similarity in bill form and other details. It resembles *C. temnura* especially. Presumably the long rictal bristles of *Platysmurus*, like those of its Malaysian associate *Platylophus*, are correlated with its jungle habitat.

With the genus *Platysmurus* we conclude the treatment of the true magpies.

PTILOSTOMUS SWAINSON (AFER)

PIAPIAC

SPECIES: 1, *afér*.

RANGE: Northern Africa south of the Palaearctic fringe.

DIAGNOSIS: Rectrices pointed, only ten present; form magpie-like; legs and feet very large; nasal bristles dense and short, meeting above the culmen; bill stout and arched; plumage black; lacrimals absent; vomer tending to be pointed anteriorly rather than truncate as in other Corvinae.

REMARKS: This is an aberrant genus whose allocation to the Corvinae has been questioned. It possesses the external characteristics of this family, such as nasal

bristles, large, strongly scutellated legs, large tenth primary, and others, and I see little reason to doubt that it is an aberrant member of the group. Jackson (1938, p. 1268) wrote that *Ptilostomus* is a gregarious, noisy bird whose notes are a "shrill and squeaky pipe" and a chattering. It feeds on palms and also on the ground where it often attends livestock. Around camp it is very tame, and Jackson thought it would make a good pet; its nidification is crow-like. These habits suggest a corvine bird. Lowe (1938, p. 261) called attention to the skull characters mentioned in the above diagnosis. I have compared the skull with that of various genera of Corvinae, and in most respects they are similar. The loss of the lacrimals and the slight distinction in the shape of the vomer, like the reduction in the number of rectrices, attest that this is an aberrant genus, but do not, in my opinion, bar inclusion in the Corvinae. Lacrimals may also be wanting in *Podoces* which is certainly a member of the Corvinae, as Lowe (*loc. cit.*) could find none in two examined specimens.

I have placed *Ptilostomus* near the end of the magpies, but its very strong legs and black coloration suggest it may be an early offshoot of the *Corvus* group. The latter has had a long history in the Ethiopian region, as witnessed by the presence there of such distinct endemic species as *C. crassirostris*, while the magpies are not represented in the Ethiopian region unless by *Ptilostomus*.

PODOCES FISCHER (PANDERI)

GROUND OR RUNNING JAYS

SYNONYMS: *Eupodoces* Sarudny and Loudon (*biddulphi*); *Pseudopodoces* Sarudny and Loudon (*humilis*).

SPECIES: 1, *hendersoni*; 2, *biddulphi*; 3, *pleskei*; 4, *panderi*; 5, *humilis*.

RANGE: High, semiarid plateaus of central Asia.

DIAGNOSIS: Derivatives of Old World jays, but highly specialized. As compared with *Garrulus*: bill attenuated and decurved; wing and tail relatively shorter and legs longer; plumage sand-colored but with wings and tail mostly bluish black as in

Garrulus and sometimes with a dark malar area as in *Garrulus*; largely terrestrial and cursorial.

REMARKS: Hartert did not recognize either of the generic synonyms listed. "*Eupodoces*" *biddulphi*, as the generic name implies, is a true *Podoces* which resembles *panderi* so closely that it is unfortunate that a generic name was applied to it. "*Pseudopodoces*" *humilis* is much more distinct, but hardly enough so to require a monotypic genus. This little bird is not larger than a bluebird (*Sialia*). It has almost lost the darker markings, but the malar region and central pair of rectrices are dull blackish. As usual in genera whose species vary considerably in size, the tenth primary is relatively shorter than in the larger species of the genus. *P. humilis* nests in rodent burrows or crevices in walls. Its eggs have become white as in many cavity-nesting species. Some of the other species of *Podoces* exceptionally nest in subterranean holes, but usually build more or less jay-like nests in bushes and lay spotted eggs. *P. humilis* looks like a lark and represents the extreme of de-differentiation and loss of corvine characters.

NUCIFRAGA BRISSON (CARYOCATACTES)

NUTCRACKERS

SYNONYM: *Picicorvus* Bonaparte (*columbiana*).
SPECIES: 1, *columbiana*; 2, *caryocatactes*.

RANGE: Mountains of Eurasia and western North America.

DIAGNOSIS: As compared with *Podoces*: bill similarly long but stouter, less decurved, and with the mandible somewhat upturned; wings and tail mostly bluish black as in *Podoces* but with some white in tail; wing relatively much longer; legs shorter; body plumage ashy or brown speckled with white.

REMARKS: *Podoces* and *Nucifraga* both seem to be descendants of Old World jay stock but whether they resemble each other sufficiently to indicate a period of common ancestry after diverging from the jays, as suggested by Menzbier and others, is a moot question. *Garrulus*, *Podoces*, and *Nucifraga* are very distinct from one another.

The two species of *Nucifraga* are rather

different; *caryocatactes* is a larger bird with much heavier bill, longer nasal bristles, and more uniform coloration than *columbiana*. Nevertheless, their similar habits and habitats and essential morphological similarity stamp them both as nutcrackers, and there is little reason to question the current practice of assigning both to *Nucifraga*. Stegmann (1934) gives reasons for considering *caryocatactes* more specialized than *columbiana* of North America; everything in their external appearance supports this conclusion. The common situation in which a primitive form survives in a peripheral area where it has escaped being overrun by successively more advanced types arising near the center of the origin of the group apparently exists in *Nucifraga*. It is, however, barely possible that the genus is of North American origin and related to *Gymnorhinus* as mentioned in discussing the latter genus.

PYRRHOCORAX TUNSTALL (PYRRHOCORAX) CHOUGHES

SYNONYM: *Graculus* Koch (*graculus*).
SPECIES: 1, *graculus*; 2, *pyrrhocrax*.

RANGE: Palaearctic region in rocky or mountainous districts.

DIAGNOSIS: Plumage glossy black; nasal bristles dense; bill and feet yellow or red; tarsus booted; bill slender and decurved; wing long; tail short; flight powerful; habits terrestrial.

REMARKS: A very distinct genus. If *Corvus* is considered to be derived from *Nucifraga*-like stock, *Pyrrhocrax* in many respects forms a link between the two. If those who consider *Corvus* to be a relative of the magpies are correct, it is difficult to judge whether *Pyrrhocrax* is correctly placed near *Corvus* or near *Nucifraga*.

In 1760 an anonymous author published a perhaps rather fanciful account of a "little bird" supposed to inhabit the Islet de Met, near Rodriguez. It is commonly supposed that he was alluding to the extinct starling, *Necropsar leguati*, of which one specimen exists. Hachisuka (1937) somehow convinced himself that this description must refer to an extinct, turtle-

eating chough, and even went so far as to name this hallucination!

ZAVATTARIOINIS MOLTONI (STRESEMANNI)

SPECIES: 1, *stresemanni* (described in 1938; no specimen seen).

RANGE: Southern Abyssinia.

DIAGNOSIS: Circumorbital area and lores unfeathered; bare skin blue in life; coloration, shape of bill, and nasal bristles about as in *Nucifraga columbiana*; size scarcely larger than in *Cyanocitta cristata*; proportions about as in the American jay, *Cyanocitta sordida*, i.e., wing rather long, tail moderate; nest large, domed, with an entrance tunnel on top.

REMARKS: Elsewhere (1943) I have summarized reasons for considering *Zavattariornis* a true member of the Corvinae. It is, however, so distinct that it is difficult to decide from published drawings, photograph, and descriptions to what living genus it is nearest in characters. Moltoni (1938) compared it with *Podoces*. The bluish black wings and tail of *Zavattariornis* suggest that it, like *Podoces* and *Nucifraga*, is a highly modified offshoot of *Garrulus*-like ancestry. The unfeathered, pigmented circumorbital area and domed nest, on the other hand, suggest the possibility that this genus, like *Philostomus*, may be an aberrant African representative of the magpies.

CORVUS LINNAEUS (CORAX)

CROWS, RAVENS, JACKDAWS

SYNONYMS: *Amblycorax* Bonaparte (*violaceus*, a race or geographical representative of *enca*); *Anomalocorax* Fitz (*splendens*); *Coleus* Kaup (*monedula*); *Corone* Kaup (*corone*); *Corvultur* Lesson (*albicollis*); *Frugilegus* Selys Longchamps (*frugilegus*); *Gymnocorvus* Lesson (*tristis*); *Heterocorax* Sharpe (*capensis*); *Microcorax* Sharpe (*jamaicensis*); *Macrocorax* Sharpe (*fuscicapillus*); *Nesocorax* Riley (*typicus*); *Physocorax* Bonaparte (*moneduloides*); *Pterocorax* Kaup (*albus*); *Rhinocorax* Sharpe (*rhripidurus*).

SPECIES: 1, *tristis*; 2, *fuscicapillus*; 3, *validus*; 4, *unicolor*; 5, *typicus*; 6, *moneduloides*; 7, *woodfordi*; 8, *meeki*; 9, *kubaryi*; 10, *enca*; 11, *splendens*; 12, *frugilegus*; 13, *monedula*; 14, *brachyrhynchus*; 15, *leucognaphalus*; 16, *ossifragus*; 17, *jamaicensis*; 18, *caurinus*; 19, *hawaiiensis*; 20, *coronoides*; 21, *orru*; 22, *bennetti*; 23, *macrorhynchus*; 24, *corone*; 25, *torquatus*; 26, *corax*; 27, *cryptoleucus*; 28,

albus; 29, *capensis*; 30, *rhripidurus*; 31, *albicollis*; 32, *crassirostris*.

RANGE: Almost cosmopolitan except in South America.

DIAGNOSIS: Large, powerfully built birds; wing relatively long; tail relatively short; coloration mostly black, rarely grayish or brownish, not infrequently with some white areas in plumage; rictal bristles long; bill and feet usually large and strong.

REMARKS: *Corvus* is the most advanced and successful genus of the Corvinae. Its large size and resilient, adaptable behavior have enabled it to exploit many secondary habitats produced by human activities. It has spread to many areas not otherwise inhabited by the group and as a result has split into almost three times as many species as any other genus of the subfamily.

Meinertzhagen (1926, pp. 57-58) has given reasons for combining all crows into one genus, though they were divided by Sharpe and others into about a dozen genera. The above arrangement is based partly on Meinertzhagen (1926) and I am also indebted to Dr. E. Mayr for assistance in the arrangement of this genus. In his opinion it is a mistake to combine the American crow (*brachyrhynchus*) specifically with *corone*, the two differing in voice and other respects. I have left the northwestern crow, *caurinus*, as a species, as it seems doubtful that it should be a race of the fish crow, *ossifragus*, of the east coast of North America.

Subgenera or other subgroups were not used by Meinertzhagen. Superficial similarity is so deceptive among the many species of this difficult genus, that the interrelationship of the species of the genus is a difficult task. A few natural subdivisions may be mentioned, however. Species 1-10 form a subgroup occupying southeastern Asia and the adjoining archipelagoes. *C. tristis* stands somewhat apart from the others by reason of partial loss of head feathers and dull coloration. *C. splendens* and *frugilegus* suggest one another in some respects, but this may be parallelism. The jackdaw, *C. monedula*, is rather distinct. In fact, Hartert left it in a monotypic genus, though most re-

cent authors have lumped *Coleus* with *Corvus*. The jackdaw is small, has a characteristic small bill, nests in cavities, and lays eggs which are rather atypical in color for the genus. The American and Hawaiian crows, species 14–19, are probably allied, as are most of the following eight species, 20–27. The African crows, species 28–32, form a natural group, with the exception of *albus* which may be an African representative of one of the Asiatic groups and perhaps should come near *torquatus*. The three last species are in some respects the most modified of the

genus. *C. rhipidurus* has a short tail. Its peculiar fan-shaped rectal bristles, as Meinertzhagen (1926, p. 96) pointed out, as well as several other characters show it to be a close relative of the large-billed *albicollis* and *crassirostris* and a link between them and other members of *Corvus*. Moreover, the bill is considerably smaller in *albicollis* than in *crassirostris* and scarcely bigger or more arched than in some of the Asiatic crows. The recognition of "*Corvultur*" seems unnecessary.

The relationship of *Corvus* to other genera is discussed below.

PHYLOGENY

The conclusions reached in the present study as to the interrelationships of the genera of Corvinae are represented in the accompanying diagram and summarized below. The jays are the most primitive subdivision. Most of the more specialized forms such as the magpies and nutcrackers seem to be variously modified jays. The jays are primitive not only morphologically but to some extent in habits, as indicated in the following quotation translated from the Heinroths (1924–1926, p. 235) based on study in the field and aviary of representatives of the genera *Garrulus*, *Nucifraga*, *Pica*, and *Corvus*: "We incline to the opinion that the jay [*Garrulus*] of all these genera has the Corvid characteristics least developed and in its behavior shows rather a certain similarity to bush-dwelling songbirds."

That the Corvinae evolved in the Old World is scarcely open to question. The groups to which they are most closely related occur exclusively in the Old World, chiefly in the tropics. Furthermore, all the more specialized genera of the Corvinae are primarily Old World, though a few of them, such as *Nucifraga*, *Pica*, and *Corvus*, have reached North America. This indicates a longer history for the subfamily in the Eastern Hemisphere, even admitting that the larger areas and perhaps more varied topography of the Old World might result in greater evolutionary advance. The primitive jay-group occurs both in the Old and New Worlds, but 32 of the approxi-

mately 38 species are American. This is evidently another instance of the type of distribution in which the primitive forms of a group have survived more abundantly in peripheral areas. In the Old World the jays have been almost eliminated by magpies, nutcrackers, and crows which are, after all, only transformed jays. In the New World there has been less competition, and the jays have undergone considerable adaptive radiation without losing their group characteristics. The very poor representation of the Corvinae in South America is another indication that the subfamily is of Old World origin.

Although the Corvinae are now well represented in both the Palaearctic and Oriental regions, the fact that closely related groups such as the birds of paradise are primarily tropical suggests that the group evolved in the Oriental region. Many forms occur in the Himalayan and Chinese mountains, which form the boundary between these regions, and it is quite possible that the Corvinae evolved in this general area and later spread both north and south. The jays, since they are the most conservative group in the subfamily, might be expected to furnish evidence on this point. *Garrulus* and *Crates* occur chiefly in temperate or boreal districts, but the former extends south well into the Oriental region, while *Crates internigrans* is endemic in the mountains of Szechwan, China. The resemblance of this species to *Garrulus lanceolatus* of the

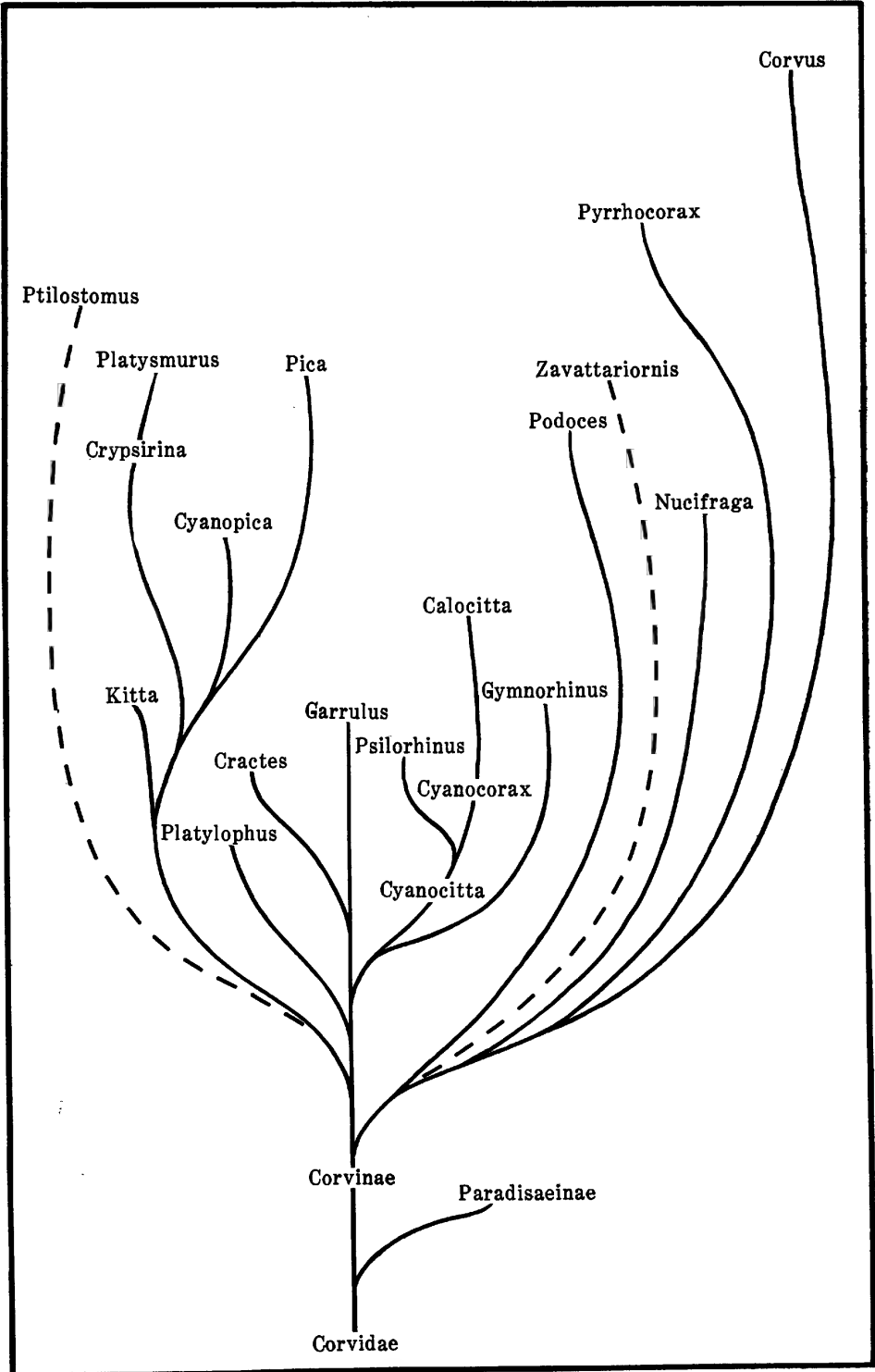


Fig. 1. Phylogeny of the Corvidae.

Himalayas is a point in favor of the suggested origin of the Corvinae in the mid-Asian mountains, since the Old World jays seem to have evolved there. *Platylophus*, the third genus of Old World jays, is entirely tropical but is aberrant and may not be a jay.

Since the Old World jays are few in number and may represent atypical forms which happen to have survived in the competition with magpies and other more advanced subgroups, the flourishing assemblage of American jays may be expected to give more reliable information as to whether the Corvinae evolved in a tropical or in a temperate region. The American jays are very predominantly tropical or subtropical. Of 32 species only six range as far north as the United States. Three of these are southern species which only cross the border into the southern United States. Another, *Cyanocitta stelleri*, ranges from Alaska to Central America; the fifth, *Gymnorhinus*, extends slightly into Mexico. Only *Cyanocitta cristata* is not found south of the United States, but it is a geographical representative of the *stelleri* group and occurs in the subtropical portions of southern Florida. On the basis of all the evidence, it seems probable that the Corvinae evolved in the tropics but that some members of the group early became adjusted to the colder climate of mountainous regions and were then able to colonize the Palaearctic and Nearctic regions.

The zoogeographical history of the jays is an interesting problem, though in the absence of fossil evidence conclusions must be very tentative. Since the New World jays are mostly tropical and the Old World jays probably were originally so, the entrance of jays into the Americas presumably occurred at a time when tropical faunas extended farther north than at present and were able to cross from Asia to North America via a Bering land bridge. The large number of tropical families common to the New and Old Worlds supplies conclusive evidence that such conditions once existed. As in most such families, the Old and New World

species of jays have become generically distinct.

Since there are jays in the temperate regions, the possibility cannot be eliminated that in this case the intercontinental transit was made by a northern jay (just as *Crates* has done more recently) which later entered the American tropics and gave rise to the genera existing there now. The genera of jays which now have a northern distribution (*Garrulus* and *Crates* of the Old World and the *Cyanocitta cristata* superspecies in the New) do not link the jays of the two hemispheres and hence offer no support to this theory. *Cyanocitta*, as Ridgway (1904, p. 346) emphasized, is related to the tropical American jays, not to *Garrulus*. The former relationship is so close that various tropical groups such as "*Cyanolyca*," formerly considered genera, have been united with *Cyanocitta* in this paper. *C. stelleri* extends south in the mountains to Central America, suggesting that it represents tropical stock which first became adjusted to colder climates in the mountains and then ranged northward and spread over the North American continent. On the other hand it may have been a temperate-zone form which was forced south in the mountains by the Pleistocene glaciation and later returned northward.

It is significant that the American jays, though primarily tropical, are a distinctly North American group. South America has no endemic genera, though two of the North American genera, *Cyanocitta* and *Cyanocorax*, occur there. The considerable radiation of the American jays must have occurred in the tropics of North America before the re-establishment of the isthmial connection between the continents in the late Tertiary. The jays thus help to validate the belief recently expressed by Simpson (1943), following earlier work by Dunn, that the tropics of North and South America are more distinct faunally, as a result of the long period in which the two continents were unconnected by land, than is generally realized.

The magpies are an Old World group of genera which are essentially large, heavy-billed, long-tailed, short-winged, often

brightly colored jays. They are birds of weak flight, adapted to forested or brushy country. The New World jays also include magpie-like types, notably *Psilorhinus* and *Calocitta*, but here the relationship is so close that generic division is difficult. In the Old World, on the other hand, two natural groups, jays and magpies, may be recognized with a perceptible but not large gap between them. The gap is most nearly bridged by *Garrulus lidhi* and *Kitta ornata*, though the resemblance of these two species is doubtless partly parallelism. Of the five genera of typical magpies, three, *Kitta*, *Crypsirina*, and *Platysmurus*, are Oriental in distribution. *Cyanopica* and *Pica* are primarily Palearctic but extend into the northern parts of the Oriental region. They are offshoots of the more primitive tropical magpies.

In response to the peculiar conditions existing in the high, barren, or brushy plateaus of central Asia, the Old World jays have produced the peculiar genus *Podoces*. Its long legs, short wings and tail, decurved bill, sandy coloration, terrestrial, cursorial habits, and other distinctive characters make the gap between *Podoces* and *Garrulus* greater than that between *Garrulus* and the magpies. Nevertheless, *Podoces* has retained enough suggestion of the color pattern and other characteristics of jays to indicate beyond much question that it was derived from jays somewhat like the existing *Garrulus*.

Nucifraga, like *Podoces*, is a transformed Old World jay. It retains the bluish black wings and tail and a suggestion of the upturned bill of *Garrulus*. The tail is short, as in *Podoces*, but since *Nucifraga* is a bird of roving habits and inhabits mountainous country, its wings are long. *Podoces* and *Nucifraga* resemble each other in a few respects, and they may have had a period of common ancestry following their divergence from the jays. They are so distinct, however, that their few similarities may only reflect the fact that both were derived from the jays. The similarity in the nasal bristles is to be attributed to the cold climate of the regions inhabited by both genera. The possibility that *Nucifraga* is related to the American genus

Gymnorhinus has been sufficiently considered in the remarks on that genus. *Nucifraga* reached North America long enough ago for the American species to become very distinct from the Palearctic one.

The recently discovered Abyssinian genus *Zavattariornis* seems to resemble *Nucifraga columbiana* more than it does any other corvid; it has been compared also with *Podoces*. It is most surprising that a relative of either genus should exist in the brushy, hot country where *Zavattariornis* occurs. *Zavattariornis* has a bare pigmented area around the eye like *Pica*, and the nest is domed as in that genus. Possibly *Zavattariornis*, despite its short tail and long bill, is a magpie. The presence of a genus of the latter in Africa would be less remarkable in view of the occurrence there of *Ptilostomus* and of *Pica* in the Palearctic fringe of northern Africa.

The thoughts of the genus *Pyrrhonorax*, like *Nucifraga*, occur in the Palearctic region and inhabit mountainous country. The two are similar in several details such as the nasal bristles, long bill, and proportions. It seems quite likely that *Pyrrhonorax* represents a further specialization of *Nucifraga*-like stock. *Pyrrhonorax* is very specialized by reason of its decurved, red bill, very long wings, booted tarsi, and black coloration.

Corvus has been considered to be related to *Pyrrhonorax*; the two are similar in proportions, color, and to some extent in habits. While this might be parallelism, it seems likely that *Corvus* evolves from the subgroup containing *Nucifraga* and *Pyrrhonorax*. The latter, despite its specializations, is intermediate between *Nucifraga* and *Corvus* in some respects.

Corvus also resembles the magpies. Shufeldt (1888) considered the skeletons of *Pica* and *Corvus* almost identical, except in size, and concluded that the two genera are closely related. The skeletons of all the Corvinae are much alike except in purely adaptive details. If *Corvus* evolved from the magpies, it must have branched off rather early in the history of that group to acquire such different proportions. The fact that *Corvus* resembles one of the most

specialized of the magpies, *Pica*, much more than it does primitive magpies, such as *Kitia*, is strongly suggestive that this is a case of parallelism rather than of close relationship.

The rather generalized characters and almost cosmopolitan distribution of *Corvus* make it difficult to determine with finality to which other genera it is most nearly allied. If related to *Pyrrhocorax* and *Nucifraga* it is, one would suppose, of Palaearctic origin. Yet the presence in Africa of perhaps the most specialized species of *Corvus* suggests the possibility that this genus evolved in Africa following the colonization of that continent by some nutcracker-like or perhaps magpie-like species. If *Corvus* is of African origin, *Ptilostomus* may well be an isolated side branch of the same stock. In any event the large size and adaptable and aggressive

nature of the species of *Corvus* have made it the most successful and widespread genus of the subfamily. The Palaearctic, Oriental, and Ethiopian regions contain many distinct species of the genus, but North America and Australia have been colonized more recently. The presence in New Zealand of remains of an extinct "crow," *Paleocorax*, would seem to indicate that the *Corvus* group reached the Australian region at a rather remote period, but it is by no means certain that *Paleocorax* is not a member of the Cracticinae.

Corvus has also reached the Philippines, Polynesia, the West Indies, and other areas not otherwise occupied by the Corvinae. Its superior colonizing ability probably derives from a combination of powerful flight and unusual ability to survive under new or unfavorable conditions.

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